CHROMOSOME STUDIES IN AMERICAN PANICOIDEAE (POACEAE)[1]

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Abstract

Chromosome numbers and observations on meiotic chromosome behavior of 37 taxa of American Panicoideae are given. The taxa studied are: *Axonopus scoparius* (Flüggé) Kuhlm., *Cenchrus myosuroides* Kunth, *Dichanthelium aciculare* var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark, *D. acuminatum* var. *acuminatum* (Sw.) Gould & C. A. Clark, *Echinochloa chacoensis* P. W. Michael ex Renvoize, *Eriochloa montevidensis* Griseb., *Isachne arundinacea* (Sw.) Griseb., *Panicum hirticaule* J. Presl, *P. stoloniferum* Poir., *P. trichanthum* Nees, *Paspalum blodgettii* Chapm., *P. buchtienii* Hack., *P. caespitosum* Flüggé, *P. candidum* (Humb. & Bonpl. ex Flüggé) Kunth, *P. ceresia* (Kuntze) Chase, *P. clavuliferum* C. Wright, *P. commune* Lillo, *P. denticulatum* Trin., *P. ekmanianum* Henrard, *P. ellipticum* Döll, *P. fimbriatum* Kunth, *P. glabrinode* (Hack.) Morrone & Zuloaga, *P. glaucescens* Hack., *P. hartwegianum* E. Fourn., *P. inconstans* Chase, *P. indecorum* Mez, *P. juergensii* Hack., *P. pauciciliatum* (Parodi) Herter, *P. penicillatum* Hook. f., *P. plicatulum* Michx., *P. prostratum* Scribn. & Merr., *P. saccharoides* Nees ex Trin., *P. squamulatum* E. Fourn., *P. variabile* (E. Fourn.) Nash, *P. wrightii* Hitchc. & Chase, *Urochloa fusca* (Sw.) B. F. Hansen & Wunderlin, and *U. lorentziana* (Mez) Morrone & Zuloaga. Nine counts are first reports for *Echinochloa chacoensis* ($2n =$ ca. 72), *Panicum stoloniferum* ($2n = 20$), *Paspalum buchtienii* ($2n = 20$), *P. ceresia* ($2n = 40$), *P. ekmanianum* ($2n = 20$), *P. glabrinode* ($2n = 20$), *P. inconstans* ($2n =$ ca. 60), *P. penicillatum* ($2n = 40$), and *P. variabile* ($2n = 40$). Ten counts differed from previously published counts: *Axonopus scoparius* ($2n = 60$), *Cenchrus myosuroides* ($2n =$ ca. 72), *Isachne arundinacea* ($2n = 20$), *Paspalum denticulatum* ($2n = 20$), *P. ellipticum* ($2n = 40$), *P. fimbriatum* ($2n =$ ca. 40), *P. hartwegianum* ($2n = 40$), *P. saccharoides* ($2n = 40$), *P. squamulatum* ($2n = 20$), and *Urochloa lorentziana* ($2n = 36$).

Key words: America, chromosome numbers, Panicoideae, Poaceae.

Knowledge of chromosome numbers and their meiotic behavior is important for understanding the phylogeny of vascular plants (Raven, 1975), particularly with regard to polyploid taxa (Davidse et al., 1986). Polyploidy is a common feature in the Poaceae, but karyological studies are still lacking in many tropical and subtropical grasses (Honfi et al., 1991), limiting our ability to understand the patterns of chromosome number change across the family. In addition, knowledge of the relationship between polyploidy and apomixis in tropical genera of grasses, such as *Dichanthelium* (Hitchc. & Chase) Gould, *Panicum* L., *Paspalum* L., and *Urochloa* P. Beauv., is necessary for plant breeding programs and for studies of reproductive systems (Connor, 1979; Quarín & Norrmann, 1987; Honfi et al., 1991; Norrmann et al., 1994).

The purpose of this work is to increase the cytological knowledge of species of Panicoideae collected in different regions of America. Chromosome counts were made in taxa of the tribe Isachneae (*Isachne*) and Paniceae (*Axonopus* P. Beauv., *Cenchrus* L., *Dichanthelium*, *Echinochloa* P. Beauv., *Eriochloa* Kunth, *Panicum*, *Paspalum*, and *Urochloa*). Chromosome numbers were compared with previous results published in the Poaceae, including the following indexes: Ornduff (1967, 1968, 1969), Bolkhovskikh et al. (1969), Moore (1970, 1971, 1972, 1973, 1974, 1977), Goldblatt (1981, 1984, 1985, 1988), and Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998, 2000).

Material and Methods

Meiosis was studied in five to 10 pollen mother cells per sample. All counts but one here reported were made from meiotic material fixed in the field with Carnoy's solution (6 parts ethanol:3 chloroform:1 acetic acid); chromosomes were stained with 2% iron propionic haematoxylin (Sáez, 1960; Núñez, 1968) and with 2% acetic carmine. Permanent slides were obtained by the dry method or by Bradley's technique (i.e., slides are dehydrated in absolute alcohol and mounted in Euparal) (Bradley, 1948). A complete list of the species, chromosome numbers, and voucher specimens studied is given in Table 1.

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Table 1. Chromosome numbers and configuration chromosome associations in taxa of American Panicoideae. *Taxa not previously cytologically studied. **Taxa with chromosome numbers that differ from previously published reports.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
***Axonopus scoparius* (Flüggé) Kuhlm.	30 II	BOLIVIA. La Paz: Prov. Nor Yungas, camino Los Yungas, alrededores de Coroico, *Morrone et al. 4209* (LPB, SI).
***Cenchrus myosuroides* Kunth	ca. 36	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, de Aeropuerto El Cadillal a SS de Jujuy, *Zuloaga & Morrone 7049* (MO, SI).
Dichanthelium aciculare var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark	9 II	MEXICO. Veracruz: Carretera 140 de Xalapa a Perote, El Acajete, *Zuloaga et al. 7442* (MEXU, SI).
Dichanthelium aciculare var. *aciculare* (Desv. ex Poir.) Gould & C. A. Clark	9 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7395* (MEXU, SI).
Dichanthelium acuminatum var. *acuminatum* (Sw.) Gould & C. A. Clark	9 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7392* (MEXU, SI).
**Echinochloa chacoensis* P. W. Michael ex Renvoize	ca. 36 II	ARGENTINA. Jujuy: Dpto. Palpalá, Ruta el algarrobal a El Cucho, *Zuloaga et al. 5848* (MO, SI).
Eriochloa montevidensis Griseb.	18 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Morrone et al. 4422* (MO, SI).
***Isachne arundinacea* (Sw.) Griseb.	10 II	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 57 km de La Paz camino a Coroico, *Morrone et al. 4192* (LPB, SI).
Panicum hirticaule J. Presl	9 II	MEXICO. Michoacán: Ruta 110, camino a Zamora pasando Villarrica, *Morrone & Giussani 3641* (MEXU, SI).
**Panicum stoloniferum* Poir.	10 II	BOLIVIA. Santa Cruz: Prov. Andrés Ibañez, 58 km de S. Cruz camino a Samaipata, *Morrone & Giussani 4268* (LPB, SI).
Panicum trichanthum Nees	18 II	ARGENTINA. Jujuy: Dpto. Santa Bárbara, 21 km de Palma Sola camino a Puesto Maíz Gordo, *Morrone et al. 4451* (MO, SI).
Paspalum blodgettii Chapm.	20 II	MEXICO. Quintana Roo: Ruta Mex-307, 43 km al S de Playa del Carmen a Tulum, *Morrone & Giussani 3658* (MEXU, SI).
**Paspalum buchtienii* Hack.	$2n = 20$	BOLIVIA. Santa Cruz: Prov. Andrés Ibañez, 58 km de Santa Cruz camino a Samaipata, *Morrone & Giussani 4258* (LPB, SI).
**Paspalum buchtienii* Hack.	10 II	BOLIVIA. La Paz: Prov. Nor Yungas, camino Los Yungas, a 63 km de La Paz camino a Coroico, *Morrone et al. 4201* (LPB, SI).
Paspalum caespitum Flüggé	10 II	MEXICO. Quintana Roo: Ruta Mex-307, 43 km al S de Playa del Carmen a Tulum, *Morrone & Giussani 3656* (MEXU, SI).
Paspalum candidum (Humb. & Bonpl. ex Flüggé) Kunth	30 II 28 II + 4 I	MEXICO. Oaxaca: San Jerónimo, *Zuloaga et al. 7396* (MEXU, SI).
**Paspalum ceresia* (Kuntze) Chase	20 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, 10 km de León camino a Tiraxi, *Morrone et al. 4386* (MO, SI).
Paspalum clavuliferum C. Wright	10 II	BRAZIL. Bahia: Mun. Mucugé, BA-142, de Mucugé a Barra da Estiva, 6 km de Mucugé, *Zuloaga & Morrone 6978* (MO, SI).

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
Paspalum commune Lillo	20 II 19 II + 2 I	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Morrone et al. 4420* (MO, SI).
***Paspalum denticulatum* Trin.	10 II	MEXICO. Puebla: Carretera de Tehuacán a Zapotitlán, km 10, cerca de Marmolera, *Zuloaga et al. 7384* (MEXU, SI).
**Paspalum ekmanianum* Henrard	10 II	ARGENTINA. Jujuy: Dpto. Dr. M. Belgrano, Palpalá, Mina 9 de Octubre, *Zuloaga et al. 5852* (MO, SI).
***Paspalum ellipticum* Döll	20 II	BRAZIL. Goiás: Alto Paraiso, *Filgueiras 3517* (IBGE, SI).
***Paspalum fimbriatum* Kunth	ca. 20 II ca. 19 II + 2 I ca. 16 II + 8 I	MEXICO. Quintana Roo: Mun. Cozumel, Isla de Cozumel, Laguna Chankanaab, *Morrone & Giussani 3651* (MEXU, SI).
**Paspalum glabrinode* (Hack.) Morrone & Zuloaga	10 II	ARGENTINA. Misiones: Dpto. San Ignacio, Peñón de La Reina Victoria, *Zuloaga & Morrone 6809* (MO, SI).
Paspalum glaucescens Hack.	20 II 19 II + 2 I 18 II + 4 I 2 IV + 13 II + 6 I	ARGENTINA. Formosa: Ruta Nac. 11, de Clorinda a Formosa, *Zuloaga & Morrone 7337* (MO, SI).
***Paspalum hartwegianum* E. Fourn.	20 II	MEXICO. Michoacán: Ruta 15d, km 159, pasando el Mun. de Maravatio, Puente Satire, *Morrone & Giussani 3612* (MEXU, SI).
**Paspalum inconstans* Chase	ca. 30 II	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 56 km de La Paz camino a Coroico, *Morrone et al. 4190* (LPB, SI).
Paspalum indecorum Mez	$2n = 20$	ARGENTINA. Misiones: Dpto. Capital, Ruta Nac. 105, de Posadas a San José, *Zuloaga & Morrone 7142* (MO, SI).
Paspalum juergensii Hack.	10 II	BOLIVIA. La Paz: Prov. Sud Yungas, a 56 km de La Paz camino a Coroico, *Morrone et al. 4188* (LPB, SI).
Paspalum pauciciliatum (Parodi) Herter	$2n =$ ca. 38	ARGENTINA. Misiones: Dpto. San Ignacio, Jardín América, *Zuloaga & Morrone 7191* (MO, SI).
**Paspalum penicillatum* Hook. f.	ca. 20 II 18 II + 4 I	BOLIVIA. La Paz: Prov. Sud Yungas, camino Los Yungas, a 57 km de La Paz camino a Coroico, *Morrone et al. 4200* (LPB, SI).
Paspalum plicatulum Michx.	10 II	MEXICO. Veracruz: Autopista de La Isla a Acayucán, km 66, *Zuloaga et al. 7418* (MEXU, SI).
Paspalum prostratum Scribn. & Merr.	ca. 20 II	MEXICO. Puebla: Carretera de Teotitlán a Huauclan, 20 km de Teotitlán, *Zuloaga et al. 7387* (MEXU, SI).
***Paspalum saccharoides* Nees ex Trin.	20 II	BOLIVIA. La Paz: Nor Yungas, a 23 km de Yolosa camino hacia Caranavi, *Morrone et al. 4211* (LPB, SI).
***Paspalum squamulatum* E. Fourn.	10 II	MEXICO. Oaxaca: Carretera de San Jerónimo a Huautla, 22 km W de Huautla, *Zuloaga et al. 7389* (MEXU, SI).
Paspalum squamulatum E. Fourn.	20 II	MEXICO. Veracruz: Carretera 140 de Xalapa a Perote, El Acajete, *Zuloaga et al. 7443* (MEXU, SI).

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
**Paspalum variabile* (E. Fourn.) Nash	20 II 19 II + 2 I	MEXICO. Oaxaca: Carretera entre San Jerónimo y Huautla, 12 km de Huautla, *Zuloaga et al. 7397* (MEXU, SI).
Paspalum wrightii Hitchc. & Chase	10 II	MEXICO. Oaxaca: Carretera Tuxtepec a Loma Bonita, 20 km de Tuxtepec, *Zuloaga et al. 7411* (MEXU, SI).
Urochloa fusca (Sw.) B. F. Hansen & Wunderlin	9 II	ARGENTINA. Jujuy: Dpto. Ledesma, Ruta Prov. 31, 7 km del desvío de la Ruta Prov. 1 camino a Vinalito, *Morrone et al. 2914* (MO, SI).
***Urochloa lorentziana* (Mez) Morrone & Zuloaga	18 II	ARGENTINA. Tucumán: Dpto. Trancas, Ruta Nac. 9, 80 km de R. de la Frontera camino a S.M. de Tucumán, *Morrone et al. 4653* (MO, SI).

Voucher specimens were deposited at the Instituto de Botánica Darwinion (SI), with duplicates at LPB, MEXU, and MO.

RESULTS AND DISCUSSION

All studied species are summarized in Table 1, including the examined configurations, voucher specimens, their provenance, and the respective collector. Collections are alphabetically ordered by genus and species and are discussed below in that order. Photomicrographs of selected species are shown in Figures 1 and 2.

Most results agreed with previously published chromosome numbers, but our counts differed for 10 species; these taxa were *Axonopus scoparius* (Flüggé) Kuhlm. ($2n = 60$), *Cenchrus myosuroides* Kunth ($2n =$ ca. 72), *Isachne arundinacea* (Sw.) Griseb. ($2n = 20$), *Paspalum denticulatum* Trin. ($2n = 20$), *P. ellipticum* Döll ($2n = 40$), *P. fimbriatum* Kunth ($2n =$ ca. 40), *P. hartwegianum* E. Fourn. ($2n = 40$), *P. saccharoides* Nees ex Trin. ($2n = 40$), *P. squamulatum* E. Fourn. ($2n = 20$), and *Urochloa lorentziana* (Mez) Morrone & Zuloaga ($2n = 36$).

Nine additional species were previously unknown cytogenetically. These first reports for chromosome number are: *Echinochloa chacoensis* P. W. Michael ex Renvoize ($2n =$ ca. 72), *Panicum stoloniferum* Poir. ($2n = 20$), *Paspalum buchtienii* Hack. ($2n = 20$), *P. ceresia* (Kuntze) Chase ($2n = 40$), *P. ekmanianum* Henrard ($2n = 20$), *P. glabrinode* (Hack.) Morrone & Zuloaga ($2n = 20$), *P. inconstans* Chase ($2n =$ ca. 60), *P. penicillatum* Hook. f. ($2n = 40$), and *P. variabile* (E. Fourn.) Nash ($2n = 40$).

Axonopus scoparius, a species of the series Barbigeri, subseries Scoparii (sensu Black, 1963), is an important natural forage grass in the Andean region. The specimen studied, from Bolivia, is a hexaploid with a count of $2n = 60$ (Fig. 1A), which differs from previous counts published by Pohl and Davidse (1971) and Shibata (1962), who reported $2n = 20$ for this species.

The widespread genus *Cenchrus*, with approximately 20 pantropical species, has base chromosome numbers of $x = 9$, 10, and 17 (Núñez, 1952; DeLisle, 1963). *Cenchrus myosuroides* has $2n =$ ca. 72, a number which differs from previous reports for this species: $2n = 54$ (Brown, 1950), $2n =$ ca. 68 (Bowden & Senn, 1962), and $2n = 70$ (Parodi, 1946; Gould, 1965; Reeder, 1968).

The American genus *Dichanthelium* includes several polymorphic complexes of uncertain specific delimitation, with different foliar and floral dimorphisms correlated with seasonal variability (Gould & Clark, 1978; Zuloaga et al., 1993). A high percentage of diploids, approximately 80%, have been reported for North and Central American species of *Dichanthelium* (Dubcovsky & Zuloaga, 1991). The genus has a base chromosome number of $x = 9$ (Brown, 1948; Gould, 1966, 1968), and the chromosome counts for *D. aciculare* (Desv. ex Poir.) Gould & C. A. Clark and *D. acuminatum* (Sw.) Gould & C. A. Clark, based on Mexican specimens, are diploid with $2n = 18$, a result that confirms previous reports for these species (Brown, 1948; Gould, 1958; Dubcovsky & Zuloaga, 1991, cited under the genus *Panicum*).

The genus *Echinochloa* includes nearly 40 species, many of them dominant in wetlands or in disturbed open areas, including cultivated fields, of tropical and temperate zones. *Echinochloa chacoensis*, a species restricted to eastern Bolivia and northern Argentina, is an octoploid with $2n =$ ca. 72, the first count for

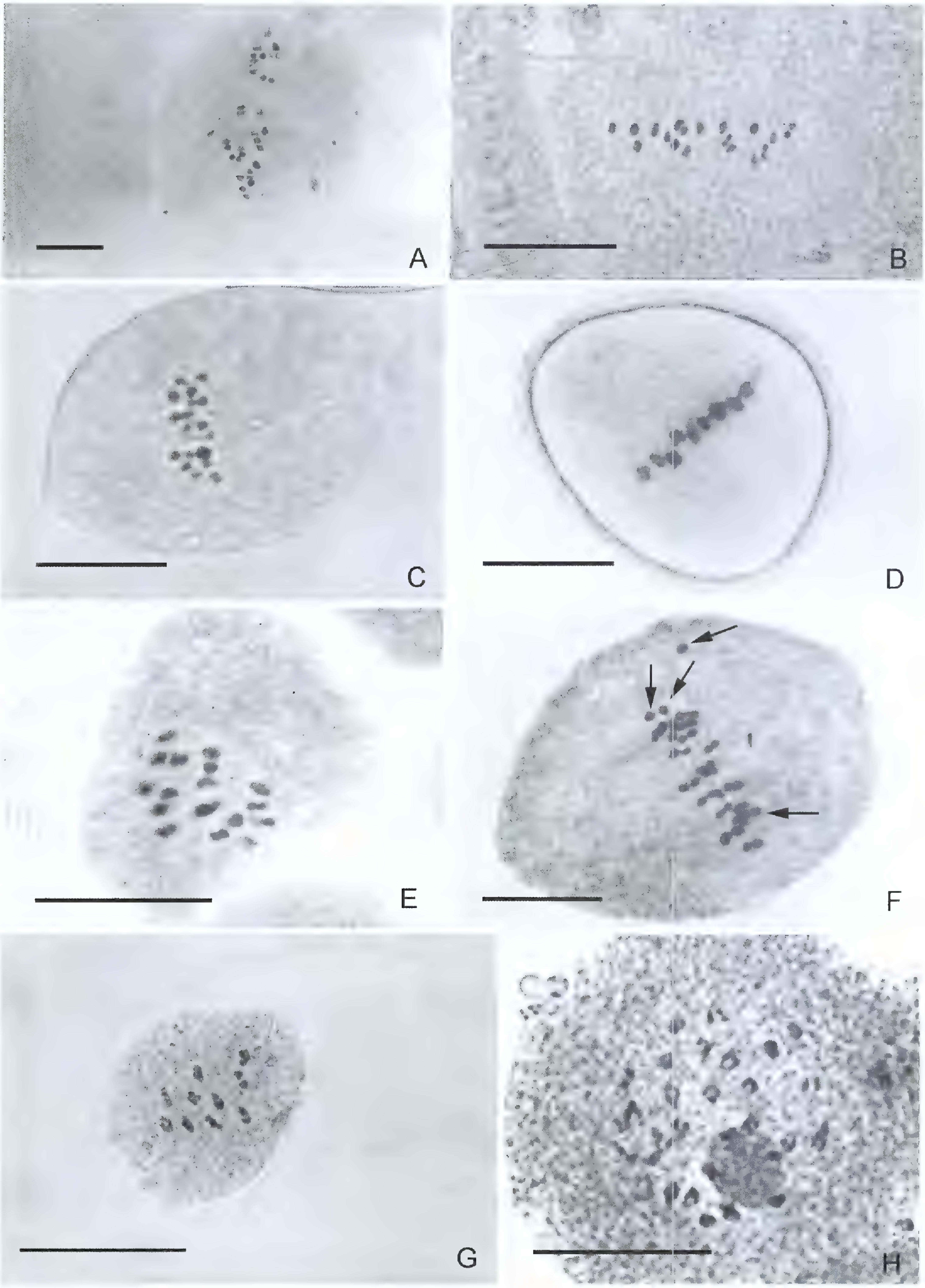

Figure 1. Photomicrographs of meiotic chromosomes of American Panicoideae. —A. *Axonopus scoparius*, 30 II, metaphase I. —B. *Eriochloa monteridensis*, 18 II, metaphase I. —C. *Panicum stoloniferum*, 10 II, prometaphase I. —D. *Paspalum glabrinode*, 10 II, metaphase I. —E. *Panicum trichanthum*, 18 II, prometaphase I. —F. *Paspalum penicillatum*, 18 II + 4 I, metaphase I. —G. *Paspalum denticulatum*, 10 II, prometaphase I. —H. *Paspalum candidum*, 30 II, diakinesis. Arrows show univalents. Scale bar = 20 μm.

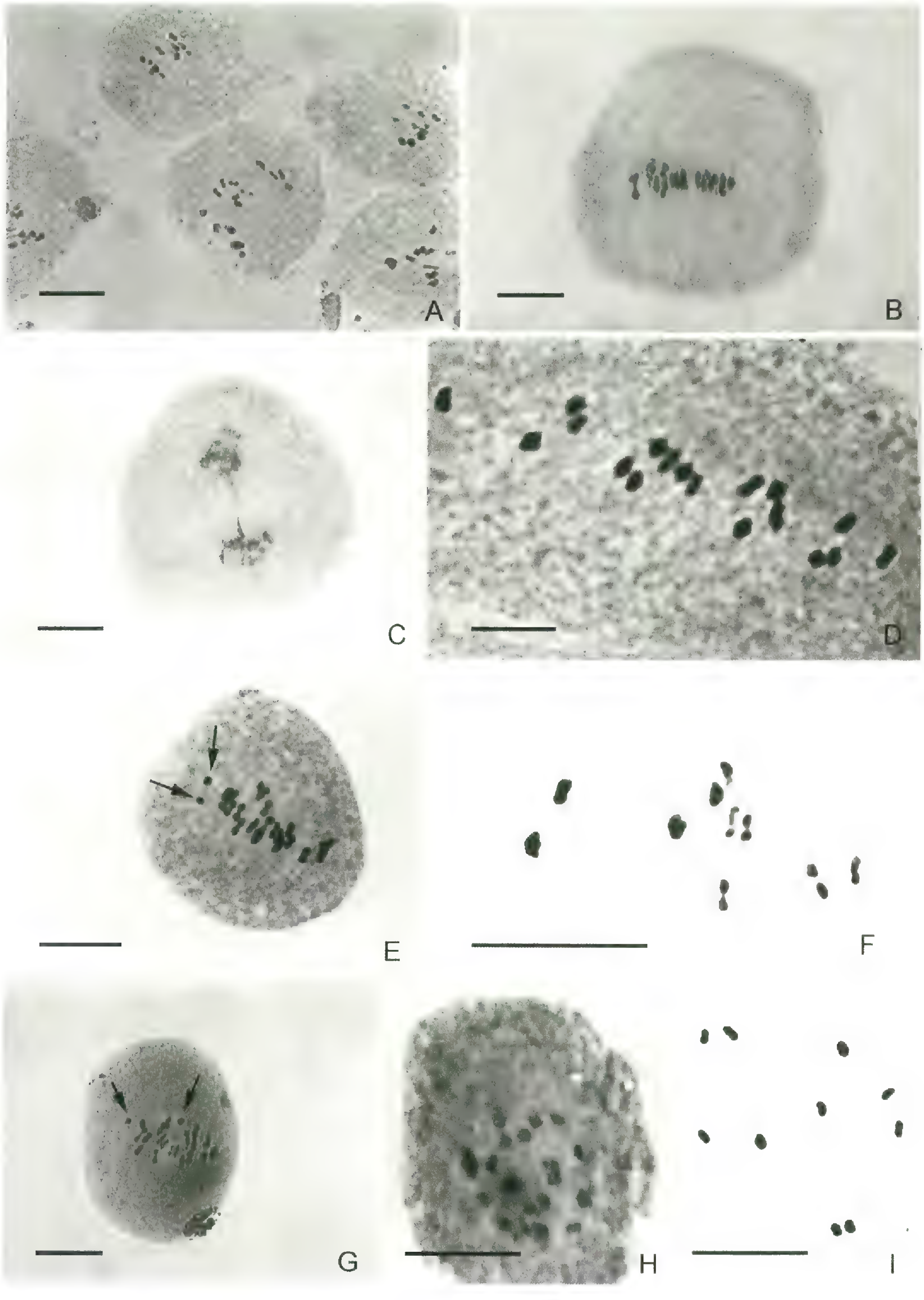

Figure 2. Photomicrographs of meiotic chromosomes of American Panicoideae. —A. *Paspalum buchtienii*, 10 II, prometaphase I. —B. *Paspalum ceresia*, 20 II, metaphase I. —C. *Paspalum commune*, bridge at anaphase II. —D. *Urochloa lorentziana*, 18 II, metaphase I. —E. *Paspalum glaucescens*, 19 II + 2 I, prometaphase I. —F. *Paspalum ekmanianum*, 10 II, metaphase I. —G. *Paspalum variabile*, 18 II + 2 I, prometaphase I. —H. *Paspalum prostratum*, ca. 20 II, diakinesis. —I. *Paspalum plicatulum*, 10 II, prometaphase I. Arrows show univalents. Scale bar = 20 μm.

this species. Polyploidy is common in *Echinochloa*, but octoploids had not been previously documented in the genus.

Eriochloa is a cosmopolitan genus with ca. 30 species present in open habitats of all continents; tetraploids, hexaploids, and octoploids have been reported in the genus. *Eriochloa montevidensis* Griseb. is a tetraploid with $2n = 36$ (Fig. 1B), a chromosome count that agrees with a previous count for the species (Núñez in Parodi, 1946); it should be mentioned that there is also a diploid count of $2n = 18$ for this species (Pohl & Davidse, 1971).

Within the pantropical genus *Isachne*, the count of a Bolivian *I. arundinacea* specimen was diploid with $2n = 20$, which differs from other published counts for this species that found individuals with $2n = 40$ (Tateoka, 1962; Davidse & Pohl, 1974).

Panicum hirticaule J. Presl, a species of subgenus *Panicum* (Zuloaga & Morrone, 1996), is a diploid with $2n = 18$, in agreement with previous results for this species (Fairbrothers, 1954; Gould, 1965; Davidse & Pohl, 1972b).

Section *Stolonifera* Hitchc. & Chase ex Pilg. of *Panicum* includes 13 American species found in the interior or at the edges of forests (Zuloaga, 1987; Zuloaga & Sendulsky, 1988). This section has been characterized as having a base chromosome number of $x = 10$, based on studies of *P. pulchellum* Raddi (Gould & Soderstrom, 1970; Pohl & Davidse, 1971; Davidse & Pohl, 1974). We here present the first chromosome count for *P. stoloniferum*, based on a specimen from Bolivia with a diploid number of $2n = 20$ (Fig. 1C).

Section *Parvifolia* Hitchc. & Chase ex Pilg. of *Panicum* has a base chromosome number of $x = 9$ (Zuloaga, 1987). A total of 31 species, found in open and moist places, are recognized from America within this section (Aliscioni et al., 2003). *Panicum trichanthum* Nees is a tetraploid with $2n = 36$ (Fig. 1E), which confirms previous counts for this species (Pohl & Davidse, 1971; Davidse & Pohl, 1972a, b, 1978; Honfi et al., 1991).

The genus *Paspalum* has approximately 310 species that are primarily American, and most have a base chromosome number of $x = 10$ (Burson, 1975). Many of these are polyploid, but most are tetraploid (Pagliarini et al., 2001). A total of 25 species were studied; of the counts recorded, 14 are new or differ from previously reported counts. Of these 25 species, 13 were tetraploids, 10 were diploids, and two were hexaploids. Chase (1929, ined.) and Zuloaga and Morrone (2005) are followed for the infrageneric arrangement of species.

Diploidy ($2n = 20$), tetraploidy ($2n = 40$), hexaploidy ($2n = 60$), and octoploidy ($2n = 80$) have been cited for subgenus *Ceresia* (Pers.) Rchb. of *Paspalum* (Saura, 1948; Tateoka, 1962; Gould & Soderstrom, 1967; Davidse & Pohl, 1972a, 1974, 1978; Pohl, 1980; Killeen, 1990; Hunziker et al., 1998). Species of this subgenus are distinguished by a winged rachis of the inflorescence, pilose spikelets, and a pale upper anthecium that is usually hyaline or membranous, with the tip of the palea not enclosed by its lemma. Two diploid counts were made for *P. buchtienii*, the first counts for this species; 10 bivalents were observed from microspore mother cells (Fig. 2A), and $2n = 20$ was observed from a mitotic metaphase of an anther wall cell. Also, the first count was made of *P. ceresia*, a tetraploid species with $2n = 40$ (Fig. 2B).

Paspalum blodgettii Chapm., *P. caespitosum* Flüggé, and *P. indecorum* Mez, species of group Caespitosa Chase, were diploid, agreeing with previously reported counts of $2n = 20$ (Davidse & Pohl, 1972a; Quarín, 1977; Quarín & Burson, 1991; Hunziker et al., 1998; Pagliarini et al., 2001), and tetraploid cytotypes, agreeing with previously reported counts of $2n = 40$ (Banks, 1964). Mexican *P. blodgettii* accessions are tetraploid with $2n = 40$, confirming a previous count by Banks (1964). Mexican *P. caespitosum* is a diploid with $2n = 20$, which agrees with determinations by Davidse and Pohl (1972a), and differs from the count reported by Banks (1964) that indicated a tetraploid cytotype with $2n = 40$. *Paspalum indecorum*, as previously reported by Quarín and Burson (1983) and Hunziker et al. (1998), is a diploid with $2n = 20$.

The group Racemosa Morrone, Zuloaga & Carbonó in *Paspalum* (Morrone et al., 1995) includes annual species of moist habitats up to 4600 m in elevation, all having the rachis flattened, deciduous, and foliaceous and the upper anthecium pale, cartilaginous, or crustaceous. Species are also anatomically characterized by having distinctive Kranz cells. Our count for the common species *P. candidum* (Humb. & Bonpl. ex Flüggé) Kunth is hexaploid with $2n = 60$ (Fig. 1H), and this agrees with several counts from Costa Rica and Honduras by Pohl and Davidse (1971) and Davidse and Pohl (1972a) but differs from previous diploid counts ($2n = 20$) (Davidse & Pohl, 1974) and tetraploid counts ($2n = 40$) (Hunziker et al., 1998). *Paspalum penicillatum* is a tetraploid with $2n = 40$, and some meiotic irregularities were observed in this species, with the presence of univalents (Fig. 1F). This is the first published count for this species. Finally, *P. prostratum* Scribn. & Merr. has $2n =$ ca. 40 (Fig. 2H), which agrees with previous studies by Davidse and Pohl (1974) and Reeder (1968). However, Pohl and Davidse (1971) also cited a hexaploid count for a Costa Rican specimen.

The Parviflora Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) consists mostly of small caespitose annuals with minute and pilose spikelets. *Paspalum clavuliferum* C. Wright was diploid, with $2n = 20$ and a regular meiosis. This count agrees with previous counts by Pohl and Davidse (1971), Davidse and Pohl, (1972a), and Reeder (1967).

The Virgata Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes tall species with a dark upper anthecium. Accessions of *P. commune* Lillo from Argentina have $2n = 40$, which confirms previous counts of this species as a tetraploid (Saura, 1941, 1948; Hunziker et al., 1998). Some meiotic anomalies resulting from an inversion heterozigosity were observed in this species, with the presence of univalents and bridges at anaphase II (Fig. 2C).

Two species were analyzed in the Livida Chase group (Chase, 1929; Zuloaga & Morrone, 2005), *Paspalum denticulatum* and *P. hartwegianum*. *Paspalum denticulatum* is a widespread American species with a high degree of variability in its vegetative and floral characters, which has led to the taxonomic establishment of several different entities now recognized under this species (Zuloaga & Morrone, 2005). *Paspalum denticulatum* was previously cited as a tetraploid with $2n = 40$ (Reeder, 1967; Gould, 1968; Davidse & Pohl, 1972b; Moraes Fernandes et al., 1974; Quarín, 1977; Quarín et al., 1982; Quarín & Burson, 1991; Hunziker et al., 1998) or a hexaploid with $2n = 60$ (Burson, 1975), but our Mexican collection was diploid ($n = 10$) (Fig. 1G). We found Mexican *P. hartwegianum* to have a count of $2n = 40$, whereas other reports had a hexaploid cytotype with $2n = 60$ (Gould, 1958; Davidse & Pohl, 1972b).

Paspalum ekmanianum, a member of the Lachnea Chase group (Chase, ined.; Zuloaga & Morrone, 2005), is an uncommon species characterized by its filiform blades and inflorescences with usually a single raceme and spikelets paired. It grows in Andean regions of southern Bolivia and northwestern Argentina, in open fields up to 2200 m in elevation. *Paspalum ekmanianum* has $2n = 20$ (Fig. 2F); this is the first reported count for this species.

The group Notata Chase of *Paspalum* (Chase, 1929; Zuloaga et al., 2004) includes caespitose perennials with inflorescences usually with two racemes and pilose or glabrous paired spikelets. The South American *P. ellipticum* was previously reported from Brazil as an octoploid (Moraes Fernandes et al., 1974), but our Brazilian collection was tetraploid, with $2n = 40$.

The group Fimbriata Chase in *Paspalum* (Chase, 1929) includes species with fimbriate spikelets, the upper glume having wings up to 3 mm long. One collection of *P. fimbriatum* was tetraploid ($2n =$ ca. 40), whereas other plants have been reported with $2n = 20$ (Banks, 1964; Gould & Soderstrom, 1967; Davidse & Pohl, 1974). Meiotic irregularities, such as the presence of 2 to 8 univalents, were observed in several cells. The meiotic behavior was normal but showed univalents in some cells, probably due to asynapsis or desynapsis at the end of diakinesis. Asynapsis occurs randomly in most individuals and is accompanied by a failure to form chiasmata, presumably caused by the interaction between the genotype and the environment.

The Decumbentes Chase group in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) is characterized by the presence of a first glume and axillary inflorescences and includes a total of 21 American species. Within it, the Argentinian species *P. glabrinode* is a diploid ($2n = 20$; Fig. 1D), the Mexican species *P. variabile* is a tetraploid ($2n = 40$; Fig. 2G), and the Bolivian species *P. inconstans* is a hexaploid ($2n =$ ca. 60). None of these species have been previously studied cytologically.

The highly polymorphic group Plicatula Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes American species distributed from the United States to Argentina that are distinguished primarily by the presence of obovoid spikelets and a dark upper anthecium. Diploid accessions of *P. plicatulum* Michx. and *P. wrightii* Hitchc. & Chase, with $2n = 20$ (Fig. 2I), were analyzed. Brown (1950), Reeder (1967), Moraes Fernandes et al. (1974), Davidse and Pohl (1972b), Honfi et al. (1991), and Martínez and Quarín (1999, under *P. hydrophilum* Henrard) reported the same number, whereas Pozzobon et al. (2000) published counts for *P. plicatulum* of $2n = 40$. This species has a striking variation in its vegetative and floral characters, a fact that has led to the establishment of many entities now synonymized under this species (Zuloaga & Morrone, 2005). Several apomictic tetraploid cytotypes have been described for *P. plicatulum* (Quarín & Norrmann, 1987). *Paspalum glaucescens* Hack. is a tetraploid with $2n = 40$, a count that is in agreement with the previous counts recorded by Moraes Fernandes et al. (1974, under *P. yaguaronense*), Pozzobon et al. (2000), and Pritchard (1962, under *P. yaguaronense* Henrard). Quadrivalents, bivalents, and univalents were observed as meiotic configurations in this species (Fig. 2E). The morphological and cytological complexities of this group indicate a need for extensive and intensive study.

The group Paniculata Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes a complex arrangement of 10 caespitose perennial species with flat blades, multiflowered inflorescences, and suborbicular spikelets. Diploid and tetraploid cytotypes have been published for the Paniculata group. The Bolivian material of *P. juergensii* Hack. was diploid with $2n = 20$, confirming the previous counts by Moraes Fernandes et al. (1974), Burson and Quarín (1982), Dandin and Chennaveeraiah (1983), Pitman et al. (1987), and Pozzobon et al. (2000). Two accessions of *P. squamulatum* from Mexico were studied. One accession is a tetraploid with $2n = 40$, in agreement with a previous report by Pohl and Davidse (1971); the second is a diploid with $2n = 20$, which differs from previous reports for this species.

The group Dilatata Chase in *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005) includes four important forage species with multiflowered inflorescences and pilose spikelets that are ciliate along the margins. *Paspalum pauciciliatum* has $2n =$ ca. 38 chromosomes; the cells observed showed restitution nuclei (Rosemberg, 1927). Previous counts for *P. pauciciliatum* include a diploid cytotype with $2n = 20$ (Moraes Fernandes et al., 1974) and a tetraploid cytotype with $2n = 40$ (Honfi et al., 1991; Pozzobon et al., 2000).

Material of *Paspalum saccharoides* from Bolivia, belonging to group Saccharoidea Chase (Chase, ined.; Zuloaga & Morrone, 2005), is tetraploid with $2n = 40$, which differs from the count reported by Pohl and Davidse (1971) for a Costa Rican specimen ($2n = 20$). *Paspalum saccharoides* is an odd species within the genus *Paspalum*. The plants are tall and scrambling to 2 m, with long and plumose inflorescences, spikelets that are long-ellipsoid and densely pilose, the upper glume and lower lemma 2-nerved and hyaline, and upper anthecium hyaline and open at the summit. Pohl and Davidse (1971) indicated similarities between spikelets of *P. saccharoides* and those of the genus *Digitaria* Haller. Nevertheless, the genus *Digitaria* has a base chromosome number of $x = 9$.

The genus *Urochloa* has approximately 110 species present in tropical and subtropical regions of the New and Old World; several species have been extensively cultivated in tropical regions. Common basic chromosome numbers in the genus are $x = 7$, 8, and 9. *Urochloa fusca* (Sw.) B. F. Hansen & Wunderlin has $2n = 18$, a count that is in agreement with previously reported counts by Gould (1958, 1966, 1968), Gould and Soderstrom (1970), Pohl and Davidse (1971), and Reeder (1971) under *Panicum fasciculatum* with $2n = 18$. *Urochloa lorentziana* is a diploid with $2n = 36$ (Fig. 2D), but previous counts indicated an arrangement of $2n = 54$ (Morrone & Zuloaga, 1992).

Literature Cited

Aliscioni, S. S., L. M. Giussani, F. O. Zuloaga & E. A. Kellogg. 2003. A molecular phylogeny of *Panicum* (Poaceae: Paniceae). Tests of monophyly and phylogenetic placement within the Panicoideae. Amer. J. Bot. 90: 796–821.

Banks, D. J. 1964. Chromosome counts for *Paspalum*. Rhodora 66: 368–370.

Black, G. A. 1963. Grasses of the genus *Axonopus* (a taxonomic treatment). Advancing Frontiers Pl. Sci. 5: 1–186.

Bolkhovskikh, Z., V. Grif, T. Matvejeva & O. Zakharyeva. 1969. Chromosome Numbers of Flowering Plants. V. L. Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg.

Bowden, W. M. & H. A. Senn. 1962. Chromosome numbers in 28 grass genera from South America. Canad. J. Bot. 40: 1115–1124.

Bradley, M. V. 1948. A method for making aceto-carmine squashes permanent without removal of the cover slip. Stain Technol. 23: 41–44.

Brown, W. V. 1948. A cytological study in the Gramineae. Amer. J. Bot. 35: 382–396.

———. 1950. A cytological study of some Texas Gramineae. Bull. Torrey Bot. Club 77: 63–76.

Burson, B. L. 1975. Cytology of some apomictic *Paspalum* species. Crop Sci. (Madison) 15: 229–232.

——— & C. L. Quarín. 1982. Cytology of *Paspalum virgatum* and relationship with *P. intermedium*, and *P. jurgensii*. Canad. J. Genet. Cytol. 24: 219–226.

Chase, A. 1929. The North American species of *Paspalum*. Contr. U.S. Natl. Herb. 28: 1–310.

———. Ined. *Revision of the South American species of genus Paspalum*. Hitchcock and Chase Library, Botany Department, Smithsonian Institution, Washington, D.C.

Connor, H. E. 1979. Breeding systems in the grasses: A survey. New Zealand J. Bot. 17: 131–154.

Dandin, S. B. & M. S. Chennaveeraiah. 1983. Chromosome number and meiotic behaviour in interpretation of basic chromosome number in the genus *Paspalum*. J. Cytol. Genet. 18: 26–33.

Davidse, G. & R. W. Pohl. 1972a. Chromosome numbers, meiotic behavior and notes on some tropical grasses from Central America and the West Indies. Canad. J. Bot. 50: 1441–1452.

——— & ———. 1972b. Chromosome numbers, meiotic behavior and notes on some grasses from Central America and the West Indies. Canad. J. Bot. 50: 273–283.

——— & ———. 1974. Chromosome numbers, meiotic behavior and notes on some tropical American grasses (Gramineae). Canad. J. Bot. 52: 371–328.

——— & ———. 1978. Chromosome numbers of tropical American grasses (Gramineae). Ann. Missouri Bot. Gard. 65: 637–649.

———, T. Hoshino & B. K. Simon. 1986. Chromosome counts of Zimbabwean grasses (Poaceae) and an analysis of polyploidy in the grass flora of Zimbabwe. S. African J. Bot. 52: 521–528.

DeLisle, D. G. 1963. Taxonomy and distribution of the genus *Cenchrus*. Iowa State Coll. J. Sci. 37: 259–351.

Dubcovsky, J. & F. O. Zuloaga. 1991 [1992]. Números cromosómicos de especies sudamericanas de *Panicum* (Poaceae: Paniceae). Bol. Soc. Argent. Bot. 27: 201–206.

Fairbrothers, D. E. 1954. Relationships in the Capillaria Group of *Panicum*. Ph.D. Dissertation, Graduate School of Cornell University, Ithaca.

Goldblatt, P. 1981. Index to plant chromosome numbers, 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–553.

———. 1984. Index to plant chromosome numbers, 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1–427.

———. 1985. Index to plant chromosome numbers, 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13: 1–224.

———. 1988. Index to plant chromosome numbers, 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 1–264.

——— & D. E. Johnson. 1990. Index to plant chromosome numbers, 1986–1987. Monogr. Syst. Bot. Missouri Bot. Gard. 30: 1–243.

——— & ———. 1991. Index to plant chromosome numbers, 1988–1989. Monogr. Syst. Bot. Missouri Bot. Gard. 40: 1–238.

——— & ———. 1994. Index to plant chromosome numbers, 1990–1991. Monogr. Syst. Bot. Missouri Bot. Gard. 51: 1–267.

——— & ———. 1996. Index to plant chromosome numbers, 1992–1993. Monogr. Syst. Bot. Missouri Bot. Gard. 58: 1–276.

——— & ———. 1998. Index to plant chromosome numbers, 1994–1995. Monogr. Syst. Bot. Missouri Bot. Gard. 69: 1–208.

——— & ———. 2000. Index to plant chromosome numbers, 1996–1997. Monogr. Syst. Bot. Missouri Bot. Gard. 81: 1–188.

Gould, F. W. 1958. Chromosome numbers in southwestern grasses. Amer. J. Bot. 45: 757–767.

———. 1965. Chromosome numbers in some Mexican grasses. Bol. Soc. Bot. México 29: 49–62.

———. 1966. Chromosome numbers of some Mexican grasses. Canad. J. Bot. 44: 1683.

———. 1968. Chromosome numbers of Texas grasses. Canad. J. Bot. 46: 1315–1325.

——— & C. F. A. Clark. 1978. *Dichanthelium* (Poaceae) in the United States and Canada. Ann. Missouri Bot. Gard. 65: 1088–1132.

——— & T. R. Soderstrom. 1967. Chromosome numbers of tropical American grasses. Amer. J. Bot. 54: 676–683.

——— & ———. 1970. Chromosome numbers of some Mexican and Colombian grasses. Canad. J. Bot. 48: 1633–1639.

Honfi, A. I., Q. L. Quarín & J. F. M. Valls. 1991 [1990]. Estudios cariológicos en gramíneas sudamericanas. Darwiniana 30: 87–94.

Hunziker, J. H., F. O. Zuloaga, O. Morrone & A. Escobar. 1998. Estudios cromosómicos en Paniceae sudamericanas (Poaceae: Panicoideae). Darwiniana 35: 29–36.

Killeen, T. J. 1990. The grasses of Chiquitanía, Santa Cruz, Bolivia. Ann. Missouri Bot. Gard. 77: 125–201.

Martínez, E. J. & C. L. Quarín. 1999. Citoembriología y comportamiento reproductivo de un citotipo diploide de *Paspalum hydrophilum* y sus híbridos con *P. palustre* (Poaceae, Paniceae). Darwiniana 37: 243–251.

Moore, R. J. 1970. Index to plant chromosome numbers for 1968. Regnum Veg. 68: 1–115.

———. 1971. Index to plant chromosome numbers for 1969. Regnum Veg. 77: 1–112.

———. 1972. Index to plant chromosome numbers for 1970. Regnum Veg. 84: 1–134.

———. 1973. Index to plant chromosome numbers for 1967–1971. Regnum Veg. 90: 1–539.

———. 1974. Index to plant chromosome numbers for 1972. Regnum Veg. 91: 1–108.

———. 1977. Index to plant chromosome numbers for 1973–1974. Regnum Veg. 96: 1–257.

Moraes Fernandes, M. I. B., I. I. Barreto, F. M. Salzano & A. M. O. F. Sacchet. 1974. Cytology and evolutionary relationships in Brazilian forms of *Paspalum* (Gramineae). Caryologia 27: 455–465.

Morrone, O. & F. O. Zuloaga. 1992. Revisión de las especies sudamericanas nativas e introducidas de los géneros *Brachiaria* y *Urochloa* (Poaceae: Panicoideae: Paniceae). Darwiniana 31: 43–109.

———, ——— & E. Carbonó. 1995. Revisión del grupo Racemosa del género *Paspalum* (Poaceae: Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 82: 82–116.

Norrmann, G. A., C. L. Quarín & T. J. Killeen. 1994. Chromosome numbers in Bolivian grasses (Gramineae). Ann. Missouri Bot. Gard. 81: 768–774.

Núñez, O. 1952. Investigaciones cariosistemáticas en las gramíneas argentinas de la tribus Paniceae. Revista Fac. Agron. Univ. Nac. La Plata 28: 229–256.

———. 1968. An acetic-haematoxilin squash method for small chromosomes. Caryologia 21: 115–119.

Ornduff, R. 1967. Index to plant chromosome numbers for 1965. Regnum Veg. 50: 1–129.

———. 1968. Index to plant chromosome numbers for 1966. Regnum Veg. 55: 1–126.

———. 1969. Index to plant chromosome numbers for 1967. Regnum Veg. 59: 1–129.

Pagliarini, M. S., L. R. Carraro, P. M. de Freitas, E. V. Adamowski, L. A. R. Batista & J. F. M. Valls. 2001. Cytogenetic characterization of Brazilian *Paspalum* accessions. Hereditas (Lund) 135: 27–34.

Parodi, L. R. 1946. Gramíneas Bonarienses. Clave para la determinación de los géneros y enumeración de las especies, 4th ed. Acme Agency, Buenos Aires.

Pitman, M. W., B. L. Burson & E. C. Bashaw. 1987. Phylogenetic relationships among *Paspalum* species with different base chromosome numbers. Bot. Gaz. 148: 130–135.

Pohl, R. W. 1980. Flora Costaricensis. Fieldiana, Bot., n.s. 4: 1–608.

——— & G. Davidse. 1971. Chromosome numbers of Costa Rican grasses. Brittonia 23: 293–324.

Pozzobon, M. T., J. F. M. Valls & S. dos Santos. 2000. Contagens cromossômicas em espécies brasileiras de *Paspalum* L. (Gramineae). Acta Bot. Brasil 14: 151–162.

Pritchard, A. J. 1962. The cytology and reproduction of *P. yaguaronense* (Henr.). Austral. J. Agric. Res. 13: 206–211.

Quarín, C. L. 1977. Recuentos cromosómicos en gramíneas de Argentina subtropical. Hickenia 1: 73–78.

——— & B. L. Burson. 1983. Cytogenetic relations among *Paspalum notatum*, *P. pumilum*, *P. indecorum* and *P. vaginatum*. Bot. Gaz. 144: 433–438.

——— & ———. 1991. Cytology of sexual and apomictic *Paspalum*. Cytologia 56: 223–228.

——— & G. A. Norrmann. 1987. Relaciones entre el número cromosómico, su comportamiento en la meiosis y el sistema reproductivo del género *Paspalum*. Anales del IV Congreso Latinoamericano de Botánica, Bogotá, Colombia 3: 25–34.

———, W. W. Hanna & A. Fernández. 1982. Genetic studies in diploid and tetraploid *Paspalum* species. J. Heredity 73: 254–256.

Raven, P. H. 1975. The basis of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

Reeder, J. R. 1967. Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bull. Torrey Bot. Club 94: 1–17.

———. 1968. Notes on Mexican grasses VIII. Miscellaneous chromosome numbers–2. Bull. Torrey Bot. Club 95: 69–86.

———. 1971. Notes on Mexican grasses. IX. Miscellaneous chromosome numbers. Brittonia 23: 105–117.

Rosemberg, O. 1927. Homeotypic division in uninucleate pollen mother cells. Hereditas (Lund) 9: 285.

Sáez, F. A. 1960. El empleo de la hematoxilina acética o propiónica para el estudio de los cromosomas con la técnica de aplastamiento. Comun. Soc. Biol. Montevideo (mimeografiado).

Saura, F. 1941. Cariología de algunas especies del género *Paspalum*. Rev. Fac. Agron. Veterin. 2: 41–48.

———. 1948. Cariología de gramíneas en Argentina. Revista Fac. Agron. Veterin. 12: 51–67.

Shibata, K. 1962. Estudio citológicos de plantas colombianas silvestres y cultivadas (Cytological studies on some wild and cultivated plants of Colombia). J. Agric. Sci. Tokyo Nogyo Daigaku, Suppl. 8: 49–62.

Tateoka, T. 1962. A cytological study of some Mexican grasses. Bull. Torrey Bot. Club 89: 77–82.

Zuloaga, F. O. 1987. Systematics of New World species of *Panicum* (Poaceae: Paniceae). Pp. 287–306 *in* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

——— & O. Morrone. 1996. Revisión de las especies americanas de *Panicum* subgénero *Panicum* sección *Panicum* (Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 83: 200–280.

——— & ———. 2005. Revisión de las especies de *Paspalum* para América del Sur Austral (Argentina, Bolivia, sur de Brasil, Chile, Paraguay y Uruguay). Monogr. Syst. Bot. Missouri Bot. Gard. 102: 1–297.

——— & T. Sendulsky. 1988. A revision of *Panicum* subgenus *Phanopyrum* section *Stolonifera* (Poaceae: Paniceae). Ann. Missouri Bot. Gard. 75: 420–455.

———, O. Morrone & R. P. Ellis. 1993. A revision of *Panicum* subg. *Dichanthelium* Sect. *Dichanthelium* (Poaceae: Panicoideae: Paniceae) in Mesoamerica, the West Indies, and South America. Ann. Missouri Bot. Gard. 80: 119–190.

———, J. Pensiero & O. Morrone. 2004. Systematics of *Paspalum* Group Notata (Poaceae-Panicoideae-Paniceae). Syst. Bot. Monogr. 71: 1–75.